ILLINOIS NATURAL HISTORY SURVEY

TECHNICAL REPORT

Historical and Contemporary Characteristics of Illinois River Valley Wetlands: A Geospatial Database for Conservation Planning and Evaluation

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Executive Summary

Large river systems and their floodplain wetlands have undergone significant degradation in the Midwestern United States. Fortunately, significant efforts to restore or enhance wetlands in these systems are ongoing, and regional conservation planners are attempting to identify habitat deficits for waterbirds to prioritize restoration objectives. Information on historical conditions of floodplain wetlands and investigations of change in conditions over time would provide valuable information to guide the restoration and planning process. To address these information needs, we first created a geospatial database of historic wetland conditions in the Illinois River valley (IRV) from maps created by Frank C. Bellrose and staff of the INHS during 1939–1959 and re-mapped 15 of these wetlands using modern techniques (i.e., Global Positioning System [GPS]) during 2005–2006. We analyzed these data to indentify changes in wetland composition and estimated energetic carrying capacity over time and factors influencing use of IRV wetlands by mallards and diving ducks based on ground and aerial inventories.

We compared wetland characteristics among 3 time periods (i.e., early historic [1939–1942], late historic [1943–1959], and contemporary [2005–2006]). Results indicated proportions of wetland area classified as bottomland forest, scrub-shrub, and mud flat were greater during 2005–2006 than the earlier mapping periods, whereas area of aquatic-bed and floating-leaved aquatic vegetation declined significantly by the contemporary period. Proportion of wetland area classified as nonpersistent emergent generally increased across all mapping periods, whereas persistent emergent area declined between the early and late historic periods. Finally, the interspersion-juxtaposition index, intended to quantify spatial heterogeneity of wetland components, was greater during the early than late mapping period, but other pairwiase comparisons were similar. Average Secchi and water depths were both significantly less during contemporary than historic mapping periods. Estimated foraging carrying capacity (i.e., duck

energy days (DED) per ha) for ducks, based on wetland composition and energetic values from Soulliere et al. (2007), did not differ significantly across mapping periods. Most models of mallard (*Anas platyrhynchos*) and diving duck abundance during 1939–1959 and 2005–2006 poorly explained variation in the dependent variables. However, models of mallard use-days considering only aerial surveys (1950–1959) indicated proportions of refuge and nonpersistent emergent vegetation, total wetland area, and the interspersion-juxtaposition index were positively associated with mallard use. Conversely, proportion of wetland classified as persistent emergent was negatively associated with the dependent variable.

We believe the general increase in percent area of nonpersistent emergent vegetation among time periods was likely due to increased moist-soil management practices, reduced water depths due to sedimentation, and substantial droughts during 2005 and 2006. However, we suggest our results indicated the loss of submersed and floating wetland vegetation further emphasizes the need to restore these components in IRV wetlands. Previous research supports our notion that these components may increase attractiveness of wetlands to many waterfowl species. Reestablishing these plant communities has been challenging in the IRV; however, we suggest successful restorations of wetlands in former drainage and levee districts isolated from the Illinois River (i.e., Hennepin-Hopper Lakes and Emiquon Preserve) provide important examples of the possibility of returning these components to some wetlands in the region.

Recent studies have improved estimates of energetic carrying capacity of waterfowl habitats. Nonetheless, we believe conservation planning would benefit from additional, large-scale studies estimating energetic availability to waterfowl across many forage types, space and time. Additionally, research identifying food densities at which foraging by waterfowl becomes unprofitable (i.e., giving-up densities) would provide information to further refine conservation objectives. Although our results indicated that energetic carrying capacity of IRV wetland did not change significantly over time, interspersion and juxtaposition of wetland components was an important predictor of historic use by mallards. We suggest that once energetic objectives for waterfowl are met, research, management, and restoration should focus on composition and spatial arrangement of vegetation to further improve wetland habitats for migrating waterfowl. Finally, most studies of waterfowl use have endeavored to identify the numerical responses of birds to wetland habitat characteristics. We believe future investigations would benefit through collection of physiological and behavioral data, thereby attempting to identify functional responses of waterfowl to restoration and management actions.

Introduction

Large river systems throughout the United States have undergone significant anthropogenic alterations during the 20th century. Although many of these changes affected the river channel itself (i.e., dredging and channelization), river floodplains usually realized greatest impacts (Bellrose et al. 1983, Sparks 1995). When the natural hydrologic ebb and flow of large floodplain rivers are altered, their lakes, backwaters, and wetlands may suffer considerable degradation and become vulnerable to development (i.e., conversion to croplands; Havera 1999). Large rivers in the upper Midwest that have undergone such alterations include the Ohio, Missouri, Mississippi, and Illinois. Fortunately, segments of these systems retain some natural hydrology, and wetland restoration and reclamation efforts are ongoing in many regions. For example, the U.S. Army Corps of Engineers has proposed spending $7.95 billion over 50 years to restore the Illinois River valley, including many backwaters, tributaries, and floodplain wetlands within the 78,000 km^2 watershed (U.S. Army Corps of Engineers 2004).

Despite extensive watershed modifications, most large river systems in the midcontinent region remain critical habitats for migrating waterbirds and other wetland dependent wildlife. Of these systems, the IRV is of primary importance to waterfowl and a focus area of the Upper Mississippi River and Great Lakes Region Joint Venture (hereafter, JV) of the North American Waterfowl Management Plan (UMRGLRJV Management Board 1998). Emphasizing its historical importance to waterfowl, 1.6 million mallards were counted during aerial inventories in the IRV in 1948, and peak numbers of lesser scaup (*Aythya affinis*) exceeded 500,000 prior to the mid-1950's (Havera 1999:227–236). An average of 20.6% of the Mississippi Flyway wintering mallard population spent at least one day in the IRV during 1955–1996 (based on midwinter inventories; Havera 1999:229). Unfortunately, extensive leveeing and drainage, primarily to promote agriculture, has eliminated 53% of the natural wetlands in the IRV (Havera 1999). Existing wetlands have been further degraded by extensive sedimentation, colonization by exotic plants and animals, and, in some cases, eutrophication from nitrogen and phosphorus. In recent years, several reclamation and restoration projects have been initiated to return structure and function of segments of the Illinois River floodplain to some former state. Some of these efforts include: 1) restoration of the Hennepin and Hopper lakes in north-central Illinois by The Wetlands Initiative; 2) dredging of Peoria Lake to remove sediment by the U.S. Army Corps of Engineers (USACOE); 3) rehabilitation of Swan (Calhoun County) and Chautauqua Lakes by the USFWS and USACOE; 4) reclamation of the 2,800 ha Emiquon Preserve by The Nature Conservancy (TNC) and the USFWS, and; 5) restoration of the Spunky Bottoms wetland area by TNC.

The goal of ecological restoration has been defined as: “The return of an ecosystem to a close approximation of its condition prior to disturbance.” (National Research Council 1992). Previous restoration efforts undoubtedly improved wetland conditions in the IRV; however, an unbiased evaluation of a return to previous conditions is difficult without detailed historical data, and this information rarely exists or is speculative. Clearly, wetland restoration efforts in the IRV and other large river systems would benefit from a database containing historical wetland conditions that are spatially and temporally referenced.

The Illinois Natural History Survey’s Forbes Biological Station possesses 140 detailed maps of IRV wetlands hand drawn and groundtruthed by or under the supervision of Frank C. Bellrose during 1938–1958 and drawn from aerial photographs in 1959. Bellrose did not produce maps for each wetland in each year; however, maps were drawn for 29 unique bottomland lakes.

These historic maps were examined by GIS experts at University of Illinois, Urbana-Champaign to determine if they were accurate and detailed enough to be scanned, georeferenced, and digitally analyzed using modern computer software. Fortunately, maps were deemed accurate and detailed enough to allow creation of a spatial database.

We believed compilation, analysis, and distribution of this historical database would provide significant guidance in evaluating restoration success of floodplain wetlands in the IRV and other large river systems in the upper Midwest. To accomplish this task we developed the following research objectives:

1. Create a GIS coverage of each historic wetland map and produce a useable database of former wetland conditions and characteristics in the IRV.
2. Return to at least half of existing wetlands to map and record present-day characteristics and include these data in the GIS database.
3. Compare wetland characteristics (i.e., vegetation composition) among "early" (e.g., 1938) and "late" (e.g., 1959) historical and contemporary (objective #2) mapping periods.
4. Estimate historical and contemporary foraging carrying capacity of these wetlands based on area of wetland vegetation and published estimates of energy values of waterfowl foods (Soulliere et al. 2007).
5. Model waterfowl use (based on existing ground and aerial inventory data) in relation to historic wetland characteristics.

The majority of our work involved addressing Objectives 1 and 2, for which we provide a DVD-ROM containing historic and contemporary GIS data (*see* cover pocket or contact: Michelle Horath, Illinois Natural History Survey, Frank C. Bellrose Waterfowl Research Center, P.O. Box 590, Havana, IL 62644; E-mail: mgeorgi@inhs.uiuc.edu). The remainder of this document provides information on field and analytical methods, results and discussion addressing Objectives 3–5.

METHODS

Development of Historic Geospatial Database

Historical maps of wetland vegetation were produced between 18 July and 16 October by Frank C. Bellrose (1938–1953) and Forrest Loomis (1955–1957) of the INHS, who used rough triangulation to plot vegetation on 1933 USACOE maps of 1:12000 scale (Bellrose 1941, Bellrose et al. 1979). Maps of wetland vegetation during August 1959 were produced from aerial photographs interpreted by Bellrose (Bellrose et al. 1979).

We digitally scanned hand-drawn vegetation maps and georectified the image using ERDAS Imagine Orthobase 8.6 and ArcGIS 9.2 software projected in the UTM coordinate system using NAD 1983, Zones 15 and 16 (Environmental Systems Research Institute 1996; Table 1). Subsequently, we digitized vegetation zones using on-screen digitizing features in ArcGIS 9.2, made spatial adjustments based on the 1933 COE maps of 1:12000 scale where necessary, and calculated the area of polygons using the XTools Pro 4.1 extension for ArcGIS (DATA East, LLC 2006).

Mapping Contemporary Wetland Characteristics

We ranked wetlands in the IRV by the number of historical map-years (the number of years a particular bottomland lake was mapped during 1938–1959) and mapped wetland vegetation (hereafter, covermapped) of 15 bottomland lakes during summers 2005 (*n* = 8; Anderson Lake, Bath Lake, Chautauqua Lake, Crane Lake, Cuba Island, Jack Lake, Moscow Bay, and Quiver Lake) and 2006 (*n* = 7; Big Lake, Clear Lake, Douglas Lake, Goose Lake

[Fulton County], Rice Lake, Sawmill Lake, and Swan Lake [Putnam County]) for which the greatest number of historical maps existed (Table 1). We identified site boundaries from historic maps created by Bellrose, present-day bluff lines, and the waterline of the Illinois River or its side channels.

We covermapped wetland vegetation using line transects (north-south or east-west UTM lines) spaced every 300 m along site perimeters. We delineated changes in vegetation structure (e.g., moist-soil, scrub-shrub, or bottomland forest) along transect lines using a GPS unit and documented dominant plant species as we transitioned between vegetation zones. We estimated plant species composition and recorded water and Secchi disc depths at 7 random locations along each transect by dividing transects into 7 equidistant segments (1 point within each segment). We established transect endpoints at the base of levees, water line of the Illinois River or side channel, or upland bluff. We traversed transects on foot, ATV, or by boat and began covermapping wetlands after the majority of wetland plants matured to aid identification (e.g., Aug. 1).

We classified wetland vegetative zones (n = 13) by grouping species of similar life forms or by the absence of vegetation (i.e., open water; OPENH2O) based on Cowardin et al. (1979). Specifically, we categorized woody vegetation as bottomland forest (FOREST) if trees were >6 m in height or scrub-shrub (SCSH) if woody vegetation was $\leq$6 m tall (Cowardin et al. 1979). We classified other wetland habitats as nonpersistent emergent vegetation (NPE; e.g., grasses and sedges), persistent emergent vegetation (PE; e.g., cattails [*Typha* spp.] and bulrushes [*Scirpus* spp.]), mud flats (MUD), floating-leaved aquatic vegetation (FLOAT; e.g., duckweed [*Lemna minor*]), and aquatic bed (AB; e.g., coontail [*Ceratophyllum demersum*]). Additionally, we believed these categories represented broad-scale wetland habitats important to migrating waterfowl (Suloway and Hubbell 1994, U.S. Fish and Wildlife Service 2007). We classified miscellaneous categories as cropland (CROP), levee (LEVEE), road (ROAD), sand (SAND), and campground (CAMP). We digitized wetland vegetation using GPS waypoints (supplemented with field notes) superimposed on 2005 and 2006 aerial photos obtained from the United States Department of Agriculture - Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/).

Statistical Analyses

Change in Wetland Characteristics.--We desired to analyze changes in wetland composition over time, but these variables were not independent due to the unit-sum constraint (i.e., all proportions sum to 1). Compositional analysis, which transforms proportional dependent variables to log-ratios, accounts for this lack of independence (Aebischer et al. 1993). However, our data set contained many zeros, and using compositional analysis would have likely lead to severely inflated Type I error rates (Bingham and Brennan 2004, Badzinski and Petrie 2006). Further, examination of residual plots indicated our errors were not multivariate-normal distributed, but arcsine square-root transforming the data did not significantly improve error distributions and complicated interpretability of results. Therefore, we selected an analytical approach similar to that of food-habits studies (Afton et al. 1991, Ross et al. 2005, Badzinski and Petrie 2006), and analyzed change in wetland habitat composition using multivariate analysis of variance (MANOVA) with simple proportions as the dependent variable. We acknowledge deviations from statistical assumptions, but consider tests appropriate because parametric multivariate analyses are considered robust to many violations of assumptions of linear models (Johnson 1995).

To compile wetland characteristics for analysis, we examined maps for continuity of site boundaries. Mapped areas varied significantly, and we desired to compare similar wetland regions over time. Thus, we clipped historic and contemporary maps in ArcGIS 9.2 to the wetland area that we believed included the regions of wetlands that received most use by waterfowl. We excluded maps from analyses if they were incomplete or not available for at least 2 of 3 categorical time periods (Table 1).

We summed wetland area (ha) of each vegetation type into the following wetland habitat categories based on Cowardin et al. (1979): 1) Bottomland Forest (FOREST); 2) Nonpersistent Emergent (NPE); 3) Open Water (OPENH2O); 4) Aquatic Bed (AB); 5) Floating-leaved Aquatic (FLOAT); 6) Mud flat (MUD); 7) Persistent Emergent (PE); 8) Scrub-shrub (SCSH); and, 9) Cropland (CROP). We computed proportions of each habitat by dividing its area by total wetland area. Further, we computed the relative richness (RR) of habitat types by dividing the number of wetland habitats present in each map by the total possible habitat types, excluding CROP ($n = 8$). Finally, wetlands with diverse habitat types distributed throughout their basins may be more valuable or attractive to waterfowl than those with clumped distributions (Weller and Spatcher 1965); therefore, we computed the Interspersion-Juxtaposition Index (IJI) for individual wetlands (McGarigal and Marks 1995). We included the IJI, the value of which increases as patches tend to be more evenly interspersed in a “salt and pepper” mixture, as an index of heterogeneity of habitat types. Procedurally, we converted all clipped wetland maps from polygons to grids (10 m cells) in ArcGIS 9.2, imported grids into ArcView 3.3, and output IJI values using the Patch Analyst v3.0 extension (Rempel and Carr 2003) via the FRAGSTATS interface (McGarigal et al. 2002).

The dependent variables in the MANOVA model included the proportion of each of 9 wetland habitat types present in each map and RR and IJI. We categorized mapping periods (independent variable) as early (1939–1942) and late (1943–1959) historic and contemporary

(2005–2006). We chose to separate historic maps into pre- and post-1942 categories because the largest flood on record in the IRV occurred in the spring of 1943. This event was a significant perturbation to floodplain wetlands of the IRV, and Bellrose et al. (1979) noted considerable changes in wetland characteristics in years following the flood as vegetation recovered.

We conducted our analysis using the MANOVA statement in PROC GLM, SAS v9.1.3, and included wetland location as a random effect to account for dependence in wetland conditions within individual wetlands (SAS Institute 2004). We used Wilk's Lambda to determine significance of the MANOVA, because it is considered robust to violations of the assumption of multivariate normality (Badzinski and Petrie 2006). If results indicated a significant ($P < 0.10$) change in wetland conditions over time, we conducted post-hoc means comparison tests using the PDIFF option within the LSMEANS statement in PROC GLM. We employed the Tukey-Kramer method to correct Type I error rate due to multiple comparisons.

Water and Secchi depth records were available for some, but not all, historic maps, whereas we recorded these depths during contemporary mapping (Table 1). Therefore, we conducted two separate analyses of variance (ANOVAs) to evaluate potential change in average water and Secchi depths (cm) between historic (1938–1959) and contemporary (2005–2006) mapping periods. We analyzed data using the MIXED procedure in SAS v9.1.3 (SAS Institute 2004), and included mapping period (TIME; 2 categories) as the independent variable and wetland location (LOC) as a random effect to account for interannual dependence among water and Secchi depth measurements within sites. We conducted post-hoc means comparison tests using the PDIFF option within the LSMEANS statement in PROC GLM (Littell et al. 1996, SAS Institute 2004).

Foraging Carrying Capacity.--Soulliere et al. (2007) identified criteria for estimating energy available to migrating and wintering waterfowl in JV wetlands. From relevant literature, the authors averaged estimates of yield (kg/ha) and true metabolizable energy of important waterfowl foods (3.0 kcal/g) to estimate energetic carrying capacity (kcal/ha) of wetland community types. Further, they divided energy estimates by 2, based on the assumption that 50% of estimated energy was actually available to waterfowl. We desired estimates of historical and contemporary energetic carrying capacity relevant to the JV; thus, we modified Soulliere et al.'s (2007) approach to include recent estimates of moist-soil plant seed abundance from the IRV (Bowyer et al. 2005, J. D. Stafford, Illinois Natural History Survey, unpublished data; Table 2).

We estimated total energy within wetlands for waterfowl from historic and contemporary maps by multiplying community-type specific energy estimates (Table 2) by the area (ha) of each habitat classification derived from ArcGIS 9.2. We computed duck energy-days (DEDs) by dividing total energy estimates by 292 (kcal/g), the assumed daily energy requirement of a mallard-sized duck during winter (Reinecke et al. 1989). Finally, we divided the previous values by total wetland area (ha) to estimate DED per-unit-area.

We evaluated potential changes in DED/ha (dependent variable) between early historic (1939–1942), late historic (1943–1959) and contemporary (2005–2006) mapping periods using mixed-models analysis of variance via the MIXED procedure in SAS v9.1.3 (SAS Institute 2004). We included mapping period (TIME) as the classified independent variable and wetland location (LOC) as a random effect to account for interannual dependence among DED estimates within sites. When a significant fixed effect was detected ($P < 0.10$) we conducted post-hoc means comparison tests using the PDIFF option within the LSMEANS statement in PROC GLM

(SAS Institute 2004). We employed the Tukey-Kramer method to correct Type I error rate due to multiple comparisons.

Ground counts and aerial inventories of waterfowl.--Beginning in 1938, Frank C. Bellrose recorded numbers of waterfowl by car and boat using binoculars and spotting scopes, typically requiring a week to inventory the IRV (Havera 1999:183). Aerial inventories began in 1948, and were conducted approximately-weekly inventories from a fixed-wing, single-engine aircraft at altitudes of 61–137 m and speeds of 161–241 km/hr (Havera 1999:186). Inventoried locations in the IRV were typically distinct floodplain lakes and associated bottomland forests and marshes that flanked the Illinois River (see Bellrose et al. 1979, 1983, and Havera 1999 for further explanation). In many cases the area surveyed was bounded by the mainstem of the Illinois River and the upland bluff, and some sites were impounded by levees. Inventoried areas of the Mississippi River included leveed wetlands within the floodplain, unleveed lateral lakes and marshes, and impounded mainstem reaches between navigation dams. We did not collect habitat-specific data on wetland use by waterfowl; rather, we estimated waterfowl abundance for the entire area of each location. Thus, each distinct complex of wetland habitats was sampled as a discrete unit.

Waterfowl use in relation to wetland characteristics.--We used the proportion of total wetland area in each of the following wetland habitat categories as covariates to explain variation in waterfowl use during historic and contemporary mapping periods (Cowardin et al. 1979): 1) Bottomland Forest (FOREST); 2) Nonpersistent Emergent (NPE); 3) Open Water (OPENH2O); 4) Aquatic Bed (AB); 5) Floating-leaved Aquatic (FLOAT); 6) Mud flat (MUD); 7) Persistent Emergent (PE); 8) Scrub-shrub (SCSH); and, 9) the Interspersion-Juxtaposition Index (*see* Page 11). Additionally, we included covariates accounting for the categorical proportion of a site where hunting and other disturbances were prohibited (i.e., 0–25%, 26–50%, 51–75%, and ≥ 76%; REFUGE; obtained by consulting Illinois Department of Natural Resources personnel; Stafford et al. 2007) and wetland size (ha; AREA) to control for the influence of these factors on duck use. We included each habitat covariate individually (with REFUGE and AREA), as well as a model intended to explain abundance of wetland plants that provide waterfowl forage (NPE+AB+FLOAT), a woody vegetation model (FOREST+SCSH), a thermal cover model (SCSH+PE), an aquatic vegetation model (AB+FLOAT) and an interspersed emergent hydrophyte (e.g., "hemi-marsh") model (IJI+NPE+PE). We did not fully parameterize any model to account for the unit-sum constraint.

We desired to model waterfowl use during entire seasons by estimating use-days (UDs) from aerial inventory or ground count data. However, aerial inventories during fall did not begin until 1948, and ground counts of waterfowl prior to this were typically limited to counts during peak migration, often with few replications. We examined available data on waterfowl abundances during the historic mapping period, and determined sufficient data was available for a subset of mapped wetlands during fall. Thus, we used aerial and ground count data to compute waterfowl USs for the period 1 October to 15 December 1939–1959, when ≥3 counts existed for a location and year, following the methods of Stafford et al. (2007:396). Waterfowl abundance data were not available for all mapped locations in 2005–2006; thus, we used data from the year wetlands were mapped when possible, otherwise we used abundance data collected during 2000, which was the most recent data available.

We developed 2 sets of candidate models to explain variation in historic fall UDs of mallards and diving ducks, respectively. Our first set of models included covariates from all maps for which ≥3 ground or aerial counts were available during 1939–1959 (n = 55; Table 1).

However, after examining results of the first modeling effort, we realized that significant outliers existed in the UD dataset, particularly during the early years computed from ground-count data (i.e., 1939–1947). These outliers contributed to considerable variation in the dependent variable (e.g., range of mallard UDs: 900–37,280,200), and resulted in poor interpretability and predictability of models. Therefore, we performed a second modeling effort using only data where aerial counts were available (1950–1959; n = 35). Because UDs computed from ground counts may have reflected real patterns in waterfowl abundance, we present both sets of models for each dependent variable so the reader may draw conclusions about the value of each model set. We only modeled mallard UDs during the contemporary period because diving duck abundance was limited during 2000–2006 aerial inventories. One site (Quiver Lake) did not receive use by either mallards or diving ducks during the study period, and we excluded it from analyses.

Regardless of mapping period (e.g., 1939–1959, 1950–1959 or 2005–2006), we modeled fall UDs using the maximum likelihood estimation method (METHOD = ML) in the MIXED procedure, SAS v9.1.3 (SAS Institute 2004). We used variance inflation factor (VIF) diagnostics to evaluate collinearity among covariates in candidate models and found no evidence of substantial intercorrelation (i.e., VIF ≤ 1.73; PROC REG; SAS Institute 2004). For historic models only, we accounted for correlation in waterfowl use among sites over time by including wetland location nested in YEAR in the REPEATED statement of PROC MIXED. We determined best approximating and competing models from our candidate set using second-order Akaike's Information Criterion (AIC_c; Burnham and Anderson 1998). We considered models competitive within candidate sets if they were ≤2.0 AIC_c units of the best approximating model. We model-averaged parameter estimates when model separation was poor and variables appeared in multiple competing models (weighted by model weight, w_i; Burnham and Anderson 1998). We interpreted importance of covariates by calculating 95% confidence intervals about parameter estimates. To evaluate model fit, we regressed observed and predicted values for each candidate model to estimate the coefficient of determination (R^2). Regardless of analytical question and statistical approach, we report all means ± 1 SE.

RESULTS

Change in Wetland Characteristics

The MANOVA model evaluating wetland habitat composition over 3 time periods was significant (Wilks' $\lambda = 0.38$; $F_{20, 182} = 5.65$, $P < 0.001$). A posteriori contrasts indicated significantly greater ($P < 0.10$) proportions of wetland classified as FOREST, SCSH and MUD during our contemporary survey compared to early and late historical periods, which did not differ (Table 3). Conversely, proportion of wetland area classified as AB was significantly less during 2005–2006 than either historical period, whereas contemporary wetlands contained significantly less area of FLOAT wetland than the early, but not late, historical period (Table 3). Proportion of NPE wetland increased significantly between the early and late historic periods and did not differ between the late historic and contemporary periods; however, the general trend in NPE increased with each time period classification (Table 3). In contrast to NPE, proportion of wetland area classified as PEM declined between early and late historical periods, but not late historical and contemporary mapping (Table 3). Proportion of OPENH2O wetland did not change over time, nor did the average relative richness of wetland categories. Finally, IJI, computed based on all wetland categories, was significantly greater in the early historic mapping period than the late historic, but average contemporary IJI was similar to both historic periods (Table 3).

Historic Secchi and water depths existed for 8 and 13 locations, respectively. Range of Historic Secchi depths were collected during 1939–1942, whereas water depth readings were available for 1938–1957. Average Secchi depth was significantly less (i.e., wetlands were more turbid; $F_{1,421} = 137.5$, $P < 0.001$; $\bar{x}$ difference = 20.6 ± 1.8 cm) during 2005–2006 ($\bar{x} = 12.4 \pm 1.8$ cm) than 1939–1942 ($\bar{x} = 33.0 \pm 2.3$ cm). Water depths were significantly shallower ($F_{1,1787}$ = 199.2, $P < 0.001$; $\bar{x}$ difference = 27.9 ± 2.0 cm) in 2005–2006 ($\bar{x} = 35.6 \pm 7.3$ cm) than 1938–1957 ($\bar{x} = 63.5 \pm 7.3$ cm).

Energetic Carrying Capacity

Estimated DED/ha did not differ among the 3 time periods ($F_{2,\,85} = 2.10$, $P = 0.129$). However, the general trend in least-squares means of average DED/ha increased between early ($\bar{x}$ = 1,061.9 ± 99.1) and late ($\bar{x}$ = 1,154.7 ± 99.6) historic and contemporary ($\bar{x}$ = 1,347.2 ± 137.2) mapping periods. Overall, wetlands in our sample provided an estimated 1,130.2 ± 53.2 DED/ha. Although significant degradation of wetland habitats for waterfowl occurred between historic and contemporary mapping periods, increased wetland area with nonpersistent emergent vegetation may have offset energetic declines, as evidenced by a strong correlation between NPE area and total wetland DEDs ($r = 0.73$).

Fall Use by Ducks in Relation to Habitat Characteristics

Mallards 1939–1959.--Four of 14 models formulated to explain variation in mallard UDs during falls 1939–1959 had ΔAIC_c values <2.0, and accounted for 76.4% of model weight (w_i; Table 4). Averaged across all competing models containing the variables, total mallard UDs were positively associated with SCSH ($\hat{\bar{\beta}}_{SCSH}$ = 601,561; 95% CI = 116,505 to 1,086,617) and AREA ($\hat{\bar{\beta}}_{AREA}$ = 5,611; 95% CI = 2,238 to 8,984). Percent OPENH2O occurred in the third best approximating model and was positively associated with mallard UDs ($\hat{\beta}_{\mathrm{OPENH2O}}$ = 66,476; 95%

CI = 12,607 to 120,345). REFUGE, FOREST and PE occurred in competing models, but 95% confidence intervals about parameter estimates did not differ from zero.

Mallards 1950–1959.--Two of 14 models in the reduced dataset intended to explain variation in mallard UDs during falls 1950–1959 were considered competitive (ΔAIC_c <2.0) and accounted for 83.5% of model weight (w_i; Table 5). Averaged across competing models, total mallard UDs were positively associated with IJI ($\hat{\bar{\beta}}_{IJI}$ = 47,390; 95% CI = 13,384 to 81,395), REFUGE ($\hat{\bar{\beta}}_{REFUGE}$ = 382,541; 95% CI = 14,548 to 750,534) and AREA ($\hat{\bar{\beta}}_{AREA}$ = 4,099; 95% CI = 3,001 to 5,197). Occurring in the best-approximating model, NPE was also positively associated with mallard UDs ($\hat{\beta}_{NPE}$ = 23,349; 95% CI = 1,301 to 45,397), whereas percent PE was negatively associated with the dependent variable ($\hat{\beta}_{PE}$= -38,013; 95% CI = -79,389 to 3,363), although the 95% CI included zero.

Mallards 2005–2006.--The best approximating model of mallard UDs during 2005–2006 included only the covariates accounting for REFUGE and AREA and accounted for 46.7% of model weight; no other model was <2.0 AIC_c units from this model (Table 6). Intuitively, REFUGE ($\hat{\beta}_{REFUGE}$ = 196,659; 95% CI = 63,375 to 329,943) and AREA ($\hat{\beta}_{AREA}$ = 381; 95% CI = 8 to 753) were positively associated with mallard UDs, although the latter parameter estimate indicated was small and the confidence interval approached zero. Although 2.2 AIC_c units from the best model, the second model accounted for 15.9% of model weight and, included the negative main effect of IJI as well as REFUGE and AREA. However, the confidence interval about parameter estimate for IJI ($\hat{\beta}_{IJI}$ = -18,429; 95% CI = -38,374 to 1,516) included zero.

Diving Ducks 1939–1959.--Separation of candidate models intended to explain variation in diving duck UDs during 1939–1959 was poor; 6 of 14 models had ΔAIC_c values <2.0, and these accounted for 71.3% of model weight (w_i; Table 7). Model-averaged parameter estimates indicated negative associations between the dependent variable and REFUGE, FOREST, and PE and positive relationships with AREA, SCSH, and OPENH2O. However, all parameter estimates were highly variable and all 95% confidence intervals about estimates included zero.

Diving Ducks 1950–1959.--Similar to modeling of mallard UDs during 1950–1959, 2 of 14 models of diving duck UDs during falls 1950–1959 were competitive and accounted for 51.1% of model weight (w_i; Table 8). The third best approximating model was 2.3 AIC$_c$ units from the best model, included only the control variables of REFUGE and AREA, and accounted for 10.1% model weight. Averaged across competing models, AREA indicated a small, positive association with fall diving duck UDs ($\hat{\bar{\beta}}_{AREA}$ = 79; 95% CI = 38 to 120), whereas the model-averaged parameter estimate for REFUGE ($\hat{\bar{\beta}}_{REFUGE}$ = 7,872; 95% CI = -6,370 to 22,114) was also positive, but the 95% confidence interval included zero. Model-averaged PE ($\hat{\bar{\beta}}_{PE}$ = -1,995; 95% CI = -3,632 to -358) was negatively associated with diving duck UDs, as was SCSH ($\hat{\beta}_{SCSH}$ = -6,549; 95% CI = -12,820 to -278), which in the best model.

DISCUSSION

Change in Wetland Composition

Researchers have been documenting deterioration of wetland habitats in the IRV for decades, and Bellrose et al. (1979) provided a comprehensive review of changes in wetland characteristics in the region. Conditions of many wetlands likely continued to decline during the subsequent 28 years, despite considerable efforts to reclaim, restore or enhance wetlands in the Illinois River floodplain. We believe our geospatial database of historic wetland conditions and analysis of the magnitude and direction of changes in wetland characteristics will provide valuable information to guide conservation planning and wetland restoration efforts.

Results of the MANOVA analysis indicated subtle changes in wetland composition between the early and late historic periods, and more dramatic changes by the contemporary period. Although not all contrasts were significant, proportion of wetlands classified as NPE generally increased across mapping periods, averaging 8.9% and 20.1% more NPE during the early than late historic and early historic than contemporary periods, respectively. Generally, NPE wetland is comprised of annual vegetation (e.g., moist-soil plants; Low and Bellrose 1944, Fredrickson and Taylor 1982) that produce seeds valuable to waterfowl. We cannot specifically account for the increased area of NPE wetland but suggest the change may have been due to: 1) increased management for moist-soil vegetation to attract waterfowl; 2) reduced water depths in wetlands due to sedimentation which likely increased wetland area favorable for growth of NPE vegetation, and; 3) uncontrollable conditions (e.g., precipitation) during the contemporary period that provided favorable hydrology for NPE vegetation. Supporting the first notion, Bellrose et al. (1979) suggested that wetland area in the IRV with the potential to control hydrology and grow moist-soil vegetation had increased due to ongoing development (e.g., construction of levees) by private hunting clubs, USACOE, USFWS, and IDNR, and it is likely this trend continued into the contemporary mapping period.

The influence of uncontrollable conditions on NPE area likely explained some of the increase in this component during the contemporary period. Significant drought prevailed during summer 2005 and a minor drought occurred in 2006 (Horath et al. 2006, Yetter et al. 2007), allowing many wetlands to dewater and maintain adequate conditions for moist-soil plant growth. Bellrose et al. (1979:47) reported frequent water level fluctuations in the IRV resulted in only 3–20% of the basin area developing moist-soil vegetation, but under most favorable water conditions 44% of the wetland area could produce moist-soil plants. Given the droughts, it was somewhat surprising that the proportion of wetlands classified as open water did not change significantly over mapping periods; however, open water area was less on average in 2005 ($\bar{x}$ = 32.6% ± 11.4%; i.e., when the drought was most severe) than 2006 ($\bar{x}$ = 43.3% ± 6.7%). Increased area of mud flat between historic and contemporary periods also may have been related to drought during 2005–2006, although sedimentation was likely a contributing factor as well. We suggest increased area of NPE during the contemporary period was at least partially a function of drought that promoted near optimum hydrologic conditions for moist-soil plant growth.

Currently, it is common knowledge that IRV wetlands are largely devoid of submersed or floating-leaved aquatic plants, and our results confirmed average area of AB and FLOAT was <0.1% during 2005–2006. These important wetland components were once relatively abundant in floodplain wetlands of the IRV (Figure 1). Interestingly, proportion of wetland area classified as AB did not differ statistically between early and late historic mapping periods (11.2% vs. 14.1%; Table 3), whereas average percent area of FLOAT declined 51.7% over the same time period (14.9% vs. 7.2%; Table 3). Correspondingly, the combined area of AB and FLOAT was generally similar between early (26.1%) and late (21.3%) historic mapping periods. Populations of migrating waterfowl declined significantly in the IRV beginning in the 1950s (Havera 1999), and the decrease may have been partially attributable to slight declines in AB and FLOAT. However, these components were still relatively abundant during the late historic mapping period. Therefore, we suspect other forces were likely responsible for declines in abundance of migratory waterfowl in the IRV.

Efforts to restore wetland areas with aquatic bed and floating-leaved aquatic vegetation in the IRV have met little success (Yin et al. 2001), but we suggest continued and increased efforts to provide habitat conducive to reestablishing these vegetation types. Restoration of submersed and floating-leaved aquatic plants is hindered in bottomland lakes connected to the Illinois River by extensive sedimentation (Starrett and Fritz 1965), fluctuating hydrology, and invasive animal species (e.g., exotic carps; Havera 1999). Wetlands with protection from some of these factors may offer opportunity to reestablish aquatic plants. Three noteworthy examples include the former Little Creek, Hennepin and Hopper, and Thompson lakes drainage and levee districts. These bottomland lakes were separated from the Illinois River during the 1920s for agriculture, but have been purchased and restored by The Wetlands Initiative (Hennepin-Hopper) and The Nature Conservancy (Little Creek [Spunky Bottoms] and Thompson Lake [Emiquon Preserve]). Both sites remain isolated from the Illinois River and this factor, combined with careful management of fish populations and water levels, likely resulted in significant beds of aquatic vegetation present at these sites. Response of waterfowl to the restoration of Hennepin-Hopper has been impressive. During 1999-2002, Hennepin-Hopper accounted for 44–66% of use-days by mallards, northern pintail (*Anas acuta*), American wigeon (*Anas americana*), gadwall (*Anas strepera*), and northern shoveler (*Anas clypeata*) in the entire Peoria Pool section of the Illinois River (Horath and Havera 2007). If detrimental effects of altered hydrology, exotic plants and animals, and sedimentation are eventually controlled, these restorations could be reconnected to the Illinois River to fully function as floodplain wetlands. Until that time, they provide important examples of successful intermediate steps to restoring aquatic plants in the region.

Generally, more wetland area classified as bottomland forest and scrub-shrub was present in contemporary than historic maps. In 1900, the Chicago Sanitary and Ship Canal was completed, diverting large amounts of water from Lake Michigan to the Illinois River (Cruikshank 1998, Havera 1999). Increased flow effectively doubled the area of bottomland lakes in the IRV (Bellrose et al. 1979:4), but killed most of the mast-producing bottomland hardwood forest (e.g., pin oaks [*Quercus palustris*], pecans [*Carya illinoensis*]) along the upper and middle portions of the IRV. Water levels remained high due to diversion until 1938, when the flow from Lake Michigan was finally reduced based on a decision by the U.S. Supreme Court (Havera et al. 1980:1–5, Havera 1999:87). Although speculative, we suggest the increased area of woody vegetation likely reflected reestablishment of mesic-tolerant trees (e.g., cottonwood [*Populus deltoides*], silver maple [*Acer saccharinum*]) and shrubs (e.g., black willow [*Salix nigra*], buttonbush [*Cephalanthus occidentalis*]) after diversion was reduced. Finally, continued sedimentation of wetlands also has almost certainly increased forested area of wetlands in the IRV (Bellrose et al. 1983).

Almost no cropland was recorded during historic mapping; however, wetland area in agricultural crops averaged 3.7% during 2005–2006. Managers of public waterfowl areas and private duck clubs often incorporate row crops into their management strategies. Although agricultural grains are considered high energy foods for waterfowl, they may lack essential amino acids found in natural plant seeds (Baldassarre et al. 1983, Delnicki and Reinecke 1986, Loesch and Kaminski 1989). Extensive agriculture in the IRV likely provides abundant waste grain for waterfowl (Warner et al. 1989), and we encourage managers to promote moist-soil or other natural wetland vegetation over agricultural crops.

Average interspersion-juxtaposition index was greater during the early than late historic and contemporary periods, though the latter difference was not statistically significant. Thus, it appears that arrangement of habitat types within wetlands was more heterogeneous early in the historic mapping period. Abundances of waterfowl during falls 1939–1942 were some of the highest recorded in the IRV. Additionally, the IJI was an important predictor in our models of mallard UDs, and we discuss the potential importance of this variable in the next section.

Energetic Carrying Capacity

Energetic and nutritional demands of waterfowl vary throughout the annual cycle and it is widely acknowledged that foods that meet the energetic requirements of migration and thermoregulation are important during autumn and winter (Baldassarre and Bolen 2006:270). Because availability of high quality forage may limit waterfowl use in the region, the JV focuses conservation planning on strategies to meet energetic requirements of wintering and migrating waterfowl by providing abundant high-energy foods (e.g., energy-based carrying capacity approach).

Our results indicated, on average, as many or more DEDs/ha were available in the Illinois River valley during 2005–2006 as during the historic periods. We believe this result is largely explained by increased area of NPE between historic and contemporary periods, as this component accounts for the greatest energy per-unit-area (Soulliere et al. 2007:37). In contrast to this result, abundance of waterfowl during fall in the IRV is currently less now than during the historic periods. Despite stable to increasing DEDs/ha, AB and FLOAT were largely extirpated from IRV wetlands prior to the contemporary period. Losses of these wetland components, resulting in more homogenous wetlands, may have reduced attractiveness to waterfowl. Submersed aquatic plants often harbor abundant and diverse invertebrate communities, thereby providing a diversity of foods beneficial to many avian-feeding niches (Hornung and Foote 2006, Longcore et al. 2006). Additionally, ducks may prefer to forage in habitats that afford predator vigilance while feeding (Guillemain et al. 2001, Fritz et al. 2002). Specifically, ducks that feed by tipping-up or with their heads submerged have no visual field and must periodically pause to scan for predators. Submersed and floating-leaved aquatic vegetation may provide forage near the surface of the water, thereby allowing dabbling ducks feed with eyes exposed and increase intake rate without sacrificing vigilance (Fritz et al. 2002). Thus, the ability to forage continually in AB or FLOAT may offset the greater energy per-unit-area of NPE that may require submersion to access forage.

Other possible explanations for the decline in waterfowl use in relation to stable energetic carrying capacity may include factors such as changes in spatial arrangement of wetland habitats, disturbance, continental population sizes, or bias in count methodology. We cannot explicitly account for this disparity, but suggest focused observational and experimental research investigating factors influencing waterfowl use of wetlands in migratory focus areas would aid conservation planning and implementation.

In Illinois, the JV endeavors to protect, restore or enhance 161,485 ha of habitat for migratory waterfowl to meet population goals (Tables 11 and 12 *in* Soulliere et al. 2007). Based on our contemporary estimate of 1,347 DED/ha, waterfowl habitat in Illinois could support about 218 million DED (i.e., UDs by mallard-sized ducks) if JV protection and restoration goals were met. This translates into enough habitat to support over 7.3 million waterfowl over a 30-day migration period. Overall, the JV endeavors to provide habitat that supports 751 million DEDs or UDs during spring migration and winter (Table 8 *in* Soulliere et al. 2007). If habitat goals were achieved, Illinois could theoretically support approximately 29% of the JV's population goal during these seasons. The majority of migratory waterfowl habitat in the state is located along the Illinois and central Mississippi rivers. Fall duck UDs in these two regions averaged 20 million during 1988–1996, with a maximum of about 80 million during 1948–1957 (Havera

1999:248). Thus, it appears available energy would exceed demand if JV habitat objectives were met.

Although it appears population goals for Illinois could be met by achieving habitat objectives, several species within the JV focus region are declining or of special concern. The JV suggested a 23 million use-day deficit in the region during the non-breeding season for greater (*Aythya marila*) and lesser scaup, corresponding with a habitat deficit of 18,854 ha (Soulliere et al. 2007:89). Likewise, research suggests that declining continental populations of Lesser Scaup may be due to changes in, or a lack of, suitable foraging habitat during spring (i.e., spring condition hypothesis; Afton and Anderson 2001, Anteau and Afton 2004, 2006, Anteau et al. 2007). Even if sufficient foraging habitat exists to meet population objectives during fall, amount of food remaining in wetlands for spring-migrating waterfowl is largely unknown. Fall-migrating waterfowl generally maintain body condition and nutrient reserve levels, but waterfowl may require additional nutrients during spring in preparation for breeding (Krapu 1981). Indeed, during springs 2004–2005 seeds were prevalent in diets of mallards and lesser scaup collected at Swan Lake on the Illinois River (Smith 2007). Greer et al. (2007) reported managed wetlands in Missouri lost 79% of seeds by spring when flooded the previous fall, whereas impoundments not flooded until spring lost only 31% of seeds. Thus, management techniques focused on providing food to spring-migrating waterfowl may mitigate fall-food losses (Greer et al. 2007). We suggest additional research investigating seasonal availability and losses of waterfowl foods would provide important information to guide conservation planning. Regardless, availability of forage during spring is critical and conservation of spring habitats should remain a high priority.

Waterfowl Use and Wetland Characteristics

We modeled UDs at mapped sites during 1939–1959 to identify variables possibly explaining variation in abundances of mallards and diving ducks; however, several factors may influence duck use concurrently. Additionally, fit of models is not implied by information criteria. Coefficients of determination for the period 1939–1959 indicated models explained modest amounts of variation in mallard UDs (R^2 = 0.34–0.44), but very little of the variation in diving duck UDs (R^2 = 0.09–0.15). Model fit improved when only aerial inventory data were considered, with models of mallard and diving duck UDs explaining 61–74% and 30–44% of variation in the dependent variables, respectively. Fit of contemporary models was better (R^2 = 0.53–0.63). We recognize that most variation in the dependent variables was explained by REFUGE and AREA, and the addition of habitat covariates resulted in only modest improvements in model fit (e.g., <14% additional variance explained; Table 5).

We cannot account for poor prediction of historic models when ground count data were included. These years included some of the highest recorded abundances of waterfowl in the IRV (Havera 1999:227). If continental populations of waterfowl were particularly great during the early historic period, one might expect use in the IRV to be relatively high as well; however, we are unaware of reliable estimates of breeding population sizes or fall flights during this period. Alternatively, counting waterfowl aerially rather than from the ground may be a more reliable way of estimating abundance (Stancill and Leslie 1990), and it is possible that ground counts did not reflect actual trends in abundance. Another possible explanation may relate to diversion of water from Lake Michigan to the Illinois River via the Chicago Sanitary and Ship Canal. Increased flow from Lake Michigan initially doubled the wetland area in the IRV, but a court order reduced flow significantly since 1939. If amount of wetland habitat for waterfowl was quickly and dramatically reduced, waterfowl arriving in the area may have been abnormally concentrated on remaining wetlands. Regardless, UD models based on data from 1939–1959 were difficult to interpret and did not perform as well as models for 1950–1959. Herein we constrain our discussion to results of models from the later period. Additionally, best models intended to predict mallard UDs during 2005–2006 included only the control variables of REFUGE and AREA or parameter estimates of other covariates were too variable to draw inference. Therefore, we devote no discussion to results of contemporary models of mallard UDs. Nonetheless, we believe habitat variables identified in our 1950–1959 analyses influenced mallard and diving duck UDs, but interpret our results cautiously and acknowledge these relationships do not imply causation.

The inclusion of REFUGE in candidate models was primarily intended to control for the effect of rest area on waterfowl use, and the association between UDs and REFUGE was intuitive and consistent with previous research findings (Stafford et al. 2007). Research in Denmark documented considerable displacement of waterfowl due to hunting, but the effect was greater when hunters were mobile rather than stationary (i.e., floating punts vs. stationary boats or blinds; Madsen 1998*a*). Hunting generally resulted in a less abundant and diverse waterfowl community and intermittent hunting (e.g., 3 days/week) did not reduce disturbance significantly unless the time between hunts was on the order of weeks (Fox and Madsen 1997; Madsen 1998*b*). Evans and Day (2002) documented greater densities of waterfowl on refuges compared to non-refuge sites during hunting season in the United Kingdom, but birds redistributed themselves among sites when hunting ceased. Havera (1999:249) reported that ducks expended 5.0–24.8% more UDs on IRV refuges during the hunting season compared to pre-season use.

We believe the predicted positive associations of REFUGE to UDs in most candidate models reaffirm the value of rest areas to waterfowl in Illinois. For example, parameterizing the best approximating models of UDs during 1950–1959 predicted that mallard use increased 23.6% and diving duck use increased 20.9% if categorical refuge area increased from 2 (26–50%) to 3 (51–75%). Bellrose (1954) described the value of waterfowl refuges in Illinois, noting that waterfowl densities were nearly 4 times greater on wetlands devoted entirely as refuge compared with sites where only half the wetland area was undisturbed. He also concluded that 26.7–52.0% of direct recoveries of waterfowl banded on Illinois refuges during fall were harvested within 40 km of the banding site (Bellrose 1954). Stafford et al. (2007) modeled use-days of mallards in the Illinois and Mississippi river valleys during 1977–1987 in relation to wetland characteristics from National Wetlands Inventory maps and reported REFUGE was an important predictor of mallard UDs during fall and spring. Specifically, models predicted average increases in fall use-days of 194,633–274,476 and increases in spring use-days of 75,654–110,720 for each 25% increase in refuge area (Stafford et al. 2007:398). The authors suggested the latter relationship perhaps indicated better spring management of, or interseasonal philopatry to, refuges (Stafford et al. 2007).

Waterfowl refuges are often intensively managed to produce vegetation that attracts birds during migration. Thus, it is possible that the significance of REFUGE in models may have been due to greater area of high-quality waterfowl habitats on refuges. However, area of PE and NPE were the best predictors of mallard UDs during 1950–1959, and a *post hoc* investigation indicated very weak relationships between these variables and REFUGE (R^2 = 0.04 [NPE and PE]); therefore, we believe lack of disturbance likely explains the relationship of REFUGE to duck use.

Our best model of mallard UDs indicated that proportion of area in emergent cover types (NPE and PE), as well as interspersion and juxtaposition of all wetland habitat types (IJI), best predicted use. The positive association with NPE during 1950–1959 was similar to results of Stafford et al. (2007), who identified combined area of PE and NPE as a positive predictor of mallard UDs during 1977–1987. Parameterizing the best approximating model of mallard UDs during 1950–1959, while holding REFUGE and AREA at the study period averages, predicted an 8.7% increase in UDs if NPE increased 5% above the study-period average ($\bar{x}$ = 22.6%). Curiously, this relationship may not hold in the contemporary landscape of the IRV. Our analysis of change in wetland characteristics over time suggested a significant increase in wetland area classified as NPE, yet estimated use-days of most duck species have been stable or declined since 1950–1959 (Havera 1999, Horath et al. 2005). Nonetheless, NPE appears to have been an important component attracting mallards to IRV wetlands during the 1950s, and we suggest our results generally support management practices that promote NPE vegetation as a means of providing quality habitat for migratory mallards.

The best model suggested that mallard UDs declined with increased proportion of wetland classified as PE, although we note the confidence interval about the parameter estimate suggested no verifiable influence. Whereas NPE vegetation typically consists of seed-producing annual plants, PE in the IRV often includes dense stands of robust emergents (e.g., river bulrush) that provide few benefits to migrating waterfowl other than thermal or escape cover.

We included the IJI in models to account for distribution of wetland habitats based on the notion that attractiveness of wetlands to some wetland-dependent avifauna may increase as compositional heterogeneity increases (*sensu* Kaminski and Prince 1981, Murkin et al. 1982, Smith et al. 2004). Indeed, our 2 best models of mallard UDs included this variable, and averaging across models indicated an average increase of 47,390 UDs for each unit increase in the IJI. Interpreting IJI can be difficult, and considerable variation existed during 1950–1959 (Range: 36.6–85.2). Thus, we refer the reader to Figure 2, which illustrate Chautauqua Lake in 1959 and 1955, when IJI values were least (45.7) and greatest (85.2) for this location.

Maximum waterfowl use and diversity has been associated with an equal interspersion of standing emergent vegetation and open water (i.e., "hemi-marsh"; Weller and Spatcher 1965, Weller and Fredrickson 1974, Kaminski and Prince 1981, Murkin et al. 1982, Smith et al. 2004). Indeed, wetlands with interspersed emergent vegetation and open water may allow for spatial segregation that minimizes competition and agonistic interactions (Kaminski and Prince 1984, Smith et al. 2004). Further, use by waterfowl may decline when proportion of emergent cover greatly exceeds open water area or vice-versa (Weller 1978, Smith et al. 2004). The IJI was computed based on all wetland habitat categories and we cannot draw inference with respect to interspersion and juxtaposition of these 2 specific types. However, these components averaged 27.7% of wetland area, and the average combined area of NPE, PE and OPENH2O was 67.4%. Whereas specific habitat types may associate with mallard use, arrangement of habitat patches within wetlands may be an important aspect of attractiveness. We believe this relationship warrants further investigation in regions of importance to staging and migrating waterfowl.

No competing model indicated a positive association of wetland habitat characteristics to diving duck UDs during falls 1950–1959. Interestingly, the parameter estimate for REFUGE indicated a positive association, as expected, but the confidence interval about the model-averaged estimate suggested the relationship was tenuous. We cannot account for the variability of this estimate, but suggest REFUGE is likely an important component of wetland management to diving ducks based on evidence that these species are particularly susceptible to disturbance (e.g., Thornburg 1973, Korschgen et al. 1985, Havera et al. 1992).

The 2 variables other than REFUGE and AREA appearing in the best approximating models of diving duck UDs indicated use declined with increased proportion of wetland area classified as PE and SCSH. These relationships are intuitive given that many diving ducks (e.g., lesser scaup, canvasback [*Aythya valisineria*]) are often associated with wetlands containing large areas of open water and shallow marsh (Korschgen 1989:159, Paracuellos 2006); thus, increasing PE and SCSH would serve to reduce open-water foraging sites. However, the lack of statistical association between diving duck UDs and AB and FLOAT was somewhat surprising. Although most wetlands contained some area of AB ($\bar{x}$ = 15.7% ± 3.4%) and FLOAT ($\bar{x}$ = 7.0% ± 2.6%) during 1950–1959, perhaps average abundance or variability of these wetland components was too low in our study areas to indicate disproportionate attractiveness to diving ducks. Alternatively, abundance of fingernail clams (e.g., *Musculium transversum*), an important food to migrating diving ducks, began to decline significantly in the IRV in the 1950s (Paloumpis and Starrett 1960, Anderson et al. 1978), concurrent with precipitous declines in diving duck abundance (Havera 1999:236). If abundance of fingernail clams was the primary attractant of diving ducks to IRV wetlands, perhaps wetland characteristics in our analysis were unable to predict diving duck use because they were not indicative of fingernail clam abundance.

SUMMARY AND IMPLICATIONS

We suggest the loss of AB and FLOAT between the late historic and contemporary mapping periods may be of greatest influence to wetland habitats and waterfowl use in the IRV. Submersed and floating vegetation was once relatively abundant in IRV wetlands, but efforts to restore these components have largely failed. Nonetheless, these wetland habitat types likely provided significant plant and animal forage for diverse guilds of migrating waterfowl.

However, our analysis of foraging carrying capacity did not suggest loss of these components resulted in reduced energy available to waterfowl in the region. Nonetheless, heterogeneity and diversity of vegetation may have enhanced the attractiveness of these wetlands to waterfowl. Although challenging, we believe that efforts to restore aquatic bed and floating-leaved aquatic plants would provide significant ecological benefits to many migratory and resident wildlife.

Energetic values of different wetland habitats used in our analysis encumbered considerable variation in methodology, space, and time (i.e., 86–13,246 DED/ha; Soulliere et al. 2007, Table 2). Due to the complexity of waterfowl foraging habitats, conservation planning and waterfowl management would benefit from studies that simultaneously estimate carrying capacity across many forage types and encompass larger spatial and temporal scales. Such an investigation would be potentially expensive and difficult to implement, but could provide information to understand how landscape-level changes and temporal variability in foraging habitats may affect waterfowl use of important migratory regions.

Recent studies have improved estimates of energetic carrying capacity for specific habitat types, such as moist-soil (Gray et al. 1999, Penny 2003, Bowyer et al. 2005, Reinecke and Hartke 2005, Kross 2006) and agricultural waste grain (Warner et. al. 1989, Stafford et al. 2006). These studies are valuable for conservation planning, but little is known about how waterfowl respond as forage is reduced, and specifically at what food densities foraging becomes unprofitable and waterfowl cease feeding or abandon wetlands (i.e., giving-up density). We are only aware of 2 estimates of giving-up densities relevant to waterfowl, both indicating mallards cease foraging in flooded rice fields when rice seed abundance drops below 50 kg/ha (Reinecke et al. 1989, Rutka 2004). The JV currently assumes half of all food is available to foraging waterfowl; this estimate is conservative, but studies identifying giving-up densities of waterfowl and pathways of seed loss (e.g., decomposition, granivory) for other important foods would allow conservation goals and objectives to be refined.

Few variables in models, other than AREA and REFUGE, explained temporal variation in mallard and diving duck UDs during fall. Certain wetland habitat types, particularly NPE, appeared to positively associate with mallard use, but even these variables explained only modest variation in UDs. Interestingly, IJI was one of the best, positive predictors of mallard UDs. We suggest this relationship indicates that once energetic goals are met (i.e., adequate forage per-unit-area), composition and arrangement of habitats within wetlands may be important attractants to waterfowl. The nature of our study was observational and we attempted to explain duck use over entire seasons. We recommend future research be conducted at finer spatial and temporal scales to better explain the relationships between duck use and wetland habitat characteristics. For example, predictive ability of models may improve if information on weather, duck abundance, vegetation structure, food availability, and disturbance were recorded daily or weekly. The previous example may improve understanding of the numerical response of waterfowl to wetland habitats, but future research should also endeavor to understand functional responses (Holling 1959). Such an approach may involve collecting data on behavior or physiological condition, and could perhaps be done experimentally (e.g., physical manipulation of forage abundance or vegetation cover).

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Table 1. Date and UTM Zone of historic and contemporary wetland maps included in the geospatial database (DVD). Check-marks denote if maps were clipped for consistent wetland area, used in specific analyses, or contained water or Secchi depth data.

Location and Year	**Date**	**UTM Zone**	**DVD**	**Clipped**	**MANOVA of Wetland Characteristics**	**Energetic Carrying Capacity**	**1939–1959 Use-day Models**	**1950–1959 Use-day Models**	**2005–2006 Use-day Models**	**Water Depths**	**Secchi Depths**
			n = 140	*n* = 129	*n* = 103	*n* = 103	*n* = 55	*n* = 36	*n* = 14	*n* = 93	*n* = 48
Anderson Lake											
1938		15	✔	✔[a]	✔	✔					
1939	27-Aug	15	✔	✔	✔	✔				✔	✔
1955	28-Sep	15	✔	✔	✔	✔	✔	✔		✔	
1956	20-Aug	15	✔	✔	✔	✔	✔	✔		✔	
1957	10-Oct	15	✔	✔	✔	✔	✔	✔		✔	
1959	Aug	15	✔	✔	✔	✔	✔	✔			
2005	Aug	15	✔	✔	✔	✔			✔	✔	✔
Babbs Slough											
1941	26-Aug	16	✔	✔[b]						✔	✔
1942	27-Aug	16	✔	✔[a]						✔	
Bath Lake											
1940	17-Aug	15	✔	✔	✔	✔					
1946	16-Oct	15	✔	✔[a]	✔	✔	✔				
1950	5-Nov	15	✔	✔	✔	✔	✔	✔			
1955	7-Sep	15	✔	✔	✔	✔	✔	✔			
1956	18-Sep	15	✔	✔	✔	✔	✔	✔			
1959	Aug	15	✔	✔	✔	✔	✔	✔			
2005	Aug	15	✔	✔	✔	✔			✔	✔	✔

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939-1959 Use-day Models	1950-1959 Use-day Models	2005-2006 Use-day Models	Water Depths	Secchi Depths
Big Lake											
1938		16	✔							✔	
1939		16	✔	✔[a]	✔	✔	✔			✔	
1940	5-Sep	16	✔	✔	✔	✔				✔	
1941	30-Jul	16	✔	✔	✔	✔	✔			✔	✔
1942	19-Aug	16	✔	✔	✔	✔	✔			✔	✔
1943	6-Oct	16	✔							✔	
1956	Sep	16	✔	✔	✔	✔	✔	✔			
2006	Aug	16	✔	✔	✔	✔			✔	✔	✔
Billsbach Lake											
1938	25-Aug	16	✔	✔						✔	
Chautauqua Lake											
1938		15	✔	✔	✔	✔					
1939		15	✔	✔	✔	✔	✔			✔	✔
1940	21-Aug	15	✔	✔	✔	✔				✔	✔
1941	6-Aug	15	✔	✔	✔	✔	✔			✔	✔
1942	11-Jul	15	✔	✔	✔	✔	✔			✔	✔
1943		15	✔	✔	✔	✔	✔				
1944		15	✔	✔	✔	✔				✔	
1946		15	✔	✔	✔	✔	✔			✔	
1953	20-Aug	15	✔								
1955	19-Sep	15	✔	✔	✔	✔	✔	✔		✔	
1956	29-Aug	15	✔	✔	✔	✔	✔	✔		✔	
1959	Aug	15	✔	✔	✔	✔	✔	✔			
2005	Aug	15	✔	✔	✔	✔			✔	✔	✔

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Clear Lake											
1939	9-Sep	16	✔	✔	✔	✔	✔				
1940	26-Aug	16	✔	✔	✔	✔				✔	
1941	1-Sep	16	✔	✔	✔	✔	✔			✔	✔
1944		16	✔	✔	✔	✔					
1950	5-Oct	16	✔								
1955	13-Oct	16	✔	✔	✔	✔	✔	✔		✔	
1959	Aug	16	✔	✔	✔	✔	✔	✔			
2006	Aug	16	✔	✔	✔	✔			✔	✔	✔
Crane Lake											
1939	17-Aug	15	✔	✔	✔	✔	✔			✔	
1940	23-Aug	15	✔	✔	✔	✔					
1941	17-Sep	15	✔	✔	✔	✔	✔				
1955	21-Sep	15	✔	✔	✔	✔	✔	✔			
1956	4-Sep	15	✔	✔[a]	✔	✔	✔	✔		✔	
2005	Sep	15	✔	✔	✔	✔			✔	✔	✔
Cuba Island											
1939	23-Aug	15	✔	✔	✔	✔				✔	✔
1942	12-Aug	15	✔	✔	✔	✔				✔	✔
1943	9-Oct	15	✔	✔	✔	✔					
1950	5-Oct	15	✔	✔[a]	✔	✔	✔				
1955	23-Sep	15	✔	✔	✔	✔	✔	✔			
1956	27-Aug	15	✔	✔	✔	✔	✔	✔		✔	
2005	Sep	15	✔	✔	✔	✔			✔	✔	✔

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Douglas Lake											
1938	8-Sep	16	✔								
1939	14-Aug	16	✔	✔	✔	✔				✔	
1940	2-Oct	16	✔	✔	✔	✔				✔	
1941	27-Aug	16	✔	✔	✔	✔	✔			✔	✔
1942		16	✔	✔	✔	✔	✔			✔	✔
1950	26-Sep	16	✔	✔	✔	✔	✔	✔		✔	✔
1956	Sep	16	✔	✔[a]	✔	✔	✔	✔			
1959	Aug	16	✔	✔	✔	✔	✔	✔			
2006	Aug	16	✔	✔	✔	✔			✔	✔	✔
Goose Lake (Fulton)											
1938	9-Aug	16	✔	✔[a]	✔	✔					
1939	16-Aug	16	✔	✔	✔	✔				✔	
1941	13-Aug	16	✔							✔	
1943	7-Oct	16	✔	✔	✔	✔					
2006	Aug	16	✔	✔	✔	✔			✔	✔	✔
Goose Lake (Putnam)											
1939	24-Sep	16	✔	✔						✔	✔
Goose Pond (Woodford)											
1941	3-Sep	16	✔	✔[a]						✔	✔
1946		16	✔	✔						✔	
Grass Lake											
1956	Sep	15	✔	✔							

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Ingram Lake											
1939	25-Aug	15	✔	✔	✔	✔				✔	✔
1955	9-Sep	15	✔	✔	✔	✔	✔	✔			
1956	6-Sep	15	✔	✔[a]	✔	✔	✔	✔		✔	
1959	Aug	15	✔	✔	✔	✔	✔	✔			
Jack Lake											
1940	7-Sep	15	✔	✔	✔	✔				✔	✔
1942	22-Aug	15	✔	✔[a]	✔	✔				✔	✔
1956	Sep	15	✔	✔	✔	✔	✔	✔			
1959	Aug	15	✔	✔	✔	✔	✔	✔			
2005	Aug	15	✔	✔	✔	✔			✔	✔	✔
Moscow Bay											
1946		15	✔								
1950	5-Nov	15	✔	✔	✔	✔	✔	✔			
1955	8-Sep	15	✔	✔	✔	✔	✔	✔			
1956	24-Sep	15	✔	✔	✔	✔	✔	✔			
1959	Aug	15	✔	✔	✔	✔	✔	✔			
2005	Aug	15	✔	✔	✔	✔			✔	✔	✔
Muscooten Bay											
1938		15	✔	✔[a]						✔	
1939	13-Sep	15	✔	✔						✔	✔
1941	14-Aug	15	✔	✔						✔	✔
Patterson Bay											
1946		15	✔	✔							

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Quiver Lake											
1938	2-Sep	15	✔	✔	✔	✔				✔	
1939	29-Aug	15	✔	✔	✔	✔				✔	
1940	6-Sep	15	✔	✔	✔	✔				✔	
1941		15	✔	✔	✔	✔					
2005	Aug	15	✔	✔	✔	✔				✔	✔
Rice Lake											
1938	30-Aug	16	✔							✔	
1939	21-Aug	16	✔	✔[b]	✔	✔				✔	
1941	19-Aug	16	✔	✔[a]	✔	✔				✔	
1942	29-Jul	16	✔	✔	✔	✔				✔	
1943	2-Oct	16	✔	✔	✔	✔	✔			✔	
1944		16	✔	✔	✔	✔				✔	
1950	5-Oct	16	✔	✔	✔	✔	✔	✔			
1953	20-Aug	16	✔								
1955	26-Sep	16	✔	✔	✔	✔	✔	✔		✔	
1956	22-Aug	16	✔	✔	✔	✔	✔	✔		✔	
1957	8-Oct	16	✔	✔	✔	✔	✔	✔		✔	
2006	Aug	16	✔	✔	✔	✔			✔	✔	✔
Sangamon Bay											
1938		15	✔	✔[a]						✔	
1939	13-Sep	15	✔	✔						✔	✔

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Sawmill Lake											
1938		16	✔							✔	
1939	15-Sep	16	✔	✔	✔	✔				✔	
1940		16	✔	✔[a]	✔	✔				✔	✔
1941	25-Aug	16	✔	✔	✔	✔				✔	✔
2006	Sep	16	✔	✔	✔	✔			✔	✔	✔
Sparland Lake											
1939		16		✔						✔	✔
1940	1-Oct	16		✔						✔	✔
1942		16		✔[a]						✔	✔
Spring Lake											
1938	12-Sep	16	✔	✔						✔	
1941		16	✔	✔[a]						✔	✔
Starved Rock Pool											
1939	3-Oct	16	✔	✔[a]							
1940	29-Sep	16	✔	✔						✔	✔
1942	15-Aug	16	✔	✔						✔	✔
Stewart Lake											
1938	1-Sep	15	✔	✔[a]						✔	
1941		15	✔	✔							

Table 1. Continued.

Location and Year	Date	UTM Zone	DVD	Clipped	MANOVA of Wetland Characteristics	Energetic Carrying Capacity	1939–1959 Use-day Models	1950–1959 Use-day Models	2005–2006 Use-day Models	Water Depths	Secchi Depths
Swan Lake (Putnam)											
1938	26-Aug	16	✔							✔	
1939	11-Sep	16	✔	✔	✔	✔	✔			✔	
1940	26-Sep	16	✔	✔	✔	✔				✔	✔
1941	25-Aug	16	✔	✔	✔	✔				✔	✔
1942	18-Jul	16	✔	✔	✔	✔				✔	
1956	Sep	16	✔	✔[a]	✔	✔	✔	✔			
2006	Sep	16	✔	✔	✔	✔			✔	✔	✔
Treadway Lake											
1938		15	✔	✔[a]						✔	
1939	16-Sep	15	✔	✔							✔
1941	14-Aug	15	✔	✔[b]						✔	✔

[a] Denotes base map used in clipping for consistent wetland area.

[b] Indicates base map was clipped back to this map for consistent wetland area.

Table 2. Estimates of energy (kcal/ha) available in general community types used by waterfowl for migration-staging and wintering in the Upper Mississippi River and Great Lakes Region Joint Venture (JV). We assumed an average true metabolizable energy (TME) estimate of 3.0 kcal/g for foods available in wetland and agricultural settings. Bold numbers are mean energy values for community types x 0.50 (0.75 for agriculture fields), assuming 50% of available energy is accessible (declining food concentration results in reduced feeding efficiency and site use). Adapted from Soulliere et al. (2007:44).

Nonpersistent Emergent	Persistent emergent	Aquatic bed	Forest and Scrub-shrub	Floating-leaved Aquatic	Open Water	Cropland
1,050,000[a]	720,000[a]	1,200,000[a]	1,110,000[a]	1,200,000[a]		
240,000[a]				25,000[a]	25,000[a]	
3,368,000[b]						
1,800,000[c]			243,000[c]			180,000[c]
						404,200[c]
958,000[d]	222,000[d]					
2,370,000[f]		1,074,000[e]		1,074,000[e]		
2,358,000[g]						
867,429	**235,500**	**568,500**	**338,000**	**383,000**	**12,500**	**219,000**

[a]Kenow et al., unpublished report, Upper Mississippi River *in* C. C. Slivinski, An assessment of the potential waterfowl carrying capacity for existing and proposed alternative refuge closed areas on Pools 4–14 of the Upper Mississippi River.

[b]Heitmeyer 1989, Agricultural/wildlife enhancement in California: The Central Valley Habitat Joint Venture. Report on general food density in California wetlands (842 kg/ha x 3,000 to convert from kg to kcal).

[c]Reinecki and Kaminski, 2005 USGS unpublished report for the Lower Mississippi Valley. Value for “bottomland hardwoods” (30% oak) was used for hemi-marsh with forest/swamp community, and waste grain includes soybeans (180,000 kcal/ha) and corn (404,200 kcal/ha, using 370 bushels/ha and 98% harvest efficiency).

[d]Steckel 2003, Food availability and waterfowl use on mid-migration habitats in central and northern Ohio.

[e]Korschgen et al. 1988, Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River.

[f]Bowyer et al. 2005, Moist-soil plant seed production for waterfowl at Chautauqua National Wildlife Refuge, Illinois.

[g]J. D. Stafford, Illinois Natural History Survey, unpublished data. Estimates of moist-soil plant seed production from public lands managed by the Illinois Department of Natural Resources.

Table 3. Results of MANOVA intended to explain variation in wetland composition over time. Means and standard errors are proportions of wetland area. Mapping periods refer to early (1939–1942) and late (1943–1959) historic and contemporary (2005–2006).

	Time Period					
	1939–1942		1943–1959		2005–2006	
Wetland Category	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Bottomland Forest	8.8A[a]	1.3	8.2A	1.3	15.3B	2.2
Nonpersistent Emergent	12.4A	2.8	21.3B	2.8	32.5B	4.8
Open Water	38.7A	3.9	41.7A	3.8	37.6A	6.6
Aquatic Bed	11.2A	2.6	14.1A	2.5	<0.1B	4.4
Floating-leaved Aquatic	14.9A	2.2	7.2B	2.1	<0.1B	3.7
Mud flat	0.4A	0.2	0.1A	0.2	1.7B	0.3
Persistent Emergent	12.3A	2.0	5.3B	2.0	3.9B	3.4
Scrub-Shrub	1.3A	0.5	2.2A	0.5	5.2B	0.8
Cropland	0.0A	0.4	0.0A	0.4	3.7B	0.7
Relative Richness	69.8A	2.1	64.2A	2.0	70.8A	3.5
Interspersion-Juxtaposition Index	69.6A	1.8	63.7B	1.7	65.8AB	3.0

[a] Values with different letters within wetland or quality index category (rows) indicate significant differences of least-squares means (Tukey-Kramer test: $P \leq 0.10$). Contrasts were based on the full multivariate model (Wilks' $\lambda = 0.38$; $F_{20,\,182} = 5.65$, $P < 0.0001$).

Table 4. Candidate models to explain variation in use-days by mallards during fall (1 October–15 December) at locations mapped by Frank C. Bellrose and inventoried from the ground or aerially for waterfowl during 1939–1959, ranked by second order Akaike's information criterion (AIC_c). Also included are the number of estimable parameters (*K*), –2 log likelihood score (–2 Log), model weight (w_i), and coefficient of determination (R^2).

Model	***K***	**-2 Log**	**AIC_c**	**ΔAIC_c**	**w_i**	**R^2**
REFUGE+FOREST+SCSH+AREA	6	1851.0	1864.8	0.0	0.253	0.437
REFUGE+SCSH+AREA	5	1853.8	1865.0	0.3	0.221	0.407
REFUGE+OPENH2O+AREA	5	1854.4	1865.6	0.9	0.164	0.401
REFUGE+SCSH+PE+AREA	6	1852.4	1866.2	1.4	0.126	0.422
REFUGE+PE+AREA	5	1856.3	1867.5	2.8	0.063	0.380
REFUGE+FOREST+AREA	5	1857.3	1868.5	3.8	0.038	0.369
REFUGE+AREA	4	1859.9	1868.7	4.0	0.035	0.338
REFUGE+IJI+AREA	5	1858.1	1869.3	4.6	0.026	0.358
REFUGE+IJI+NPE+PE+AREA	7	1853.0	1869.4	4.6	0.025	0.416
REFUGE+AB+AREA	5	1858.7	1869.9	5.2	0.019	0.353
REFUGE+NPE+AREA	5	1859.8	1871.0	6.3	0.011	0.339
REFUGE+FLOAT+AREA	5	1859.8	1871.0	6.3	0.011	0.339
REFUGE+AB+FLOAT+AREA	6	1858.6	1872.4	7.6	0.006	0.353
REFUGE+NPE+AB+FLOAT+AREA	7	1857.4	1873.8	9.0	0.003	0.367

Table 5. Candidate models to explain variation in use-days by mallards during fall (1 October–15 December) at locations mapped by Frank C. Bellrose and inventoried aerially for waterfowl during 1950–1959, ranked by second order Akaike's information criterion (AIC$_c$). Also included are the number of estimable parameters (K), –2 log likelihood score (–2 Log), model weight (w_i), and coefficient of determination (R^2).

Model	K	**-2 Log**	**AIC$_c$**	**ΔAIC$_c$**	w_i	R^2
REFUGE+IJI+NPE+PE+AREA	7	1109.2	1127.2	0.0	0.500	0.742
REFUGE+IJI+AREA	5	1116.0	1128.0	0.8	0.335	0.689
REFUGE+NPE+AREA	5	1119.3	1131.3	4.1	0.064	0.659
REFUGE+PE+AREA	5	1120.4	1132.4	5.2	0.037	0.648
REFUGE+AREA	4	1124.5	1133.8	6.6	0.019	0.606
REFUGE+SCSH+PE+AREA	6	1120.3	1135.2	8.0	0.009	0.649
REFUGE+FLOAT+AREA	5	1123.9	1135.9	8.7	0.006	0.612
REFUGE+AB+AREA	5	1124.0	1136.0	8.8	0.006	0.611
REFUGE+SCSH+AREA	5	1124.0	1136.0	8.8	0.006	0.611
REFUGE+FOREST+AREA	5	1124.3	1136.3	9.1	0.005	0.608
REFUGE+OPENH2O+AREA	5	1124.4	1136.4	9.2	0.005	0.606
REFUGE+NPE+AB+FLOAT+AREA	7	1118.8	1136.8	9.6	0.004	0.663
REFUGE+AB+FLOAT+AREA	6	1123.7	1138.6	11.4	0.002	0.615
REFUGE+FOREST+SCSH+AREA	6	1123.9	1138.8	11.6	0.002	0.612

Table 6. Candidate models to explain variation in use-days by mallards during fall (1 October–15 December) at locations mapped The staff of the Forbes Biological Station and inventoried aerially for waterfowl during 2000–2006, ranked by second order Akaike's information criterion (AIC_c). Also included are the number of estimable parameters (K), –2 log likelihood score (–2 Log), model weight (w_i), and coefficient of determination (R^2).

Model	K	**-2 Log**	AIC_c	ΔAIC_c	w_i	R^2
REFUGE+AREA	4	390.7	403.1	0.0	0.467	0.525
REFUGE+IJI+AREA	5	387.8	405.3	2.2	0.159	0.616
REFUGE+FOREST+AREA	5	388.8	406.3	3.2	0.096	0.587
REFUGE+SCSH+AREA	5	389.4	406.9	3.8	0.071	0.570
REFUGE+PE+AREA	5	390.4	407.9	4.8	0.043	0.537
REFUGE+NPE+AREA	5	390.7	408.2	5.1	0.037	0.527
REFUGE+FLOAT+AREA	5	390.7	408.2	5.1	0.037	0.528
REFUGE+AB+AREA	5	390.7	408.2	5.1	0.037	0.528
REFUGE+OPENH2O+AREA	5	390.7	408.2	5.1	0.037	0.525
REFUGE+FOREST+SCSH+AREA	6	387.2	411.2	8.1	0.008	0.630
REFUGE+SCSH+PE+AREA	6	389.3	413.3	10.2	0.003	0.572
REFUGE+AB+FLOAT+AREA	6	390.6	414.6	11.5	0.002	0.531
REFUGE+IJI+NPE+PE+AREA	7	387.5	420.2	17.0	0.000	0.623
REFUGE+NPE+AB+FLOAT+AREA	7	390.5	423.2	20.0	0.000	0.532

Table 7. Candidate models to explain variation in use-days by diving ducks during fall (1 October–15 December) at locations mapped by Frank C. Bellrose and inventoried from the ground or aerially for waterfowl during 1939–1959, ranked by second order Akaike's information criterion (AIC_c). Also included are the number of estimable parameters (K), –2 log likelihood score (–2 Log), model weight (w_i), and coefficient of determination (R^2).

Model	K	**-2 Log**	AIC_c	ΔAIC_c	w_i	R^2
REFUGE+AREA	4	1566.5	1575.3	0.0	0.170	0.088
REFUGE+FOREST+AREA	5	1564.4	1575.6	0.3	0.145	0.121
REFUGE+SCSH+AREA	5	1564.9	1576.1	0.8	0.113	0.114
REFUGE+OPENH2O+AREA	5	1565.1	1576.3	1.0	0.102	0.111
REFUGE+PE+AREA	5	1565.3	1576.5	1.2	0.092	0.107
REFUGE+FOREST+SCSH+AREA	6	1562.8	1576.6	1.3	0.091	0.146
REFUGE+NPE+AREA	5	1566.3	1577.5	2.2	0.056	0.091
REFUGE+AB+AREA	5	1566.4	1577.6	2.3	0.053	0.089
REFUGE+FLOAT+AREA	5	1566.4	1577.6	2.3	0.053	0.088
REFUGE+IJI+AREA	5	1566.4	1577.6	2.3	0.053	0.088
REFUGE+SCSH+PE+AREA	6	1564.4	1578.2	2.9	0.041	0.121
REFUGE+AB+FLOAT+AREA	6	1566.4	1580.2	4.9	0.015	0.089
REFUGE+NPE+AB+FLOAT+AREA	7	1566.0	1582.4	7.1	0.005	0.096
REFUGE+IJI+NPE+PE+AREA	7	1564.7	1581.1	5.8	0.009	0.116

Table 8. Candidate models to explain variation in use-days by diving ducks during fall (1 October–15 December) at locations mapped by Frank C. Bellrose and inventoried aerially for waterfowl during 1950–1959, ranked by second order Akaike's information criterion (AIC_c). Also included are the number of estimable parameters (K), –2 log likelihood score (–2 Log), model weight (w_i), and coefficient of determination (R^2).

Model	***K***	**-2 Log**	**AIC_c**	**ΔAIC_c**	**w_i**	**R^2**
REFUGE+SCSH+PE+AREA	6	875.3	890.2	0.0	0.318	0.436
REFUGE+PE+AREA	5	879.2	891.2	1.0	0.193	0.371
REFUGE+AREA	4	883.2	892.5	2.3	0.101	0.297
REFUGE+NPE+AREA	5	881.0	893.0	2.8	0.078	0.339
REFUGE+SCSH+AREA	5	881.5	893.5	3.3	0.061	0.330
REFUGE+IJI+AREA	5	881.6	893.6	3.4	0.058	0.328
REFUGE+FLOAT+AREA	5	882.5	894.5	4.3	0.037	0.310
REFUGE+IJI+NPE+PE+AREA	7	876.5	894.5	4.3	0.037	0.416
REFUGE+AB+AREA	5	883.1	895.1	4.9	0.027	0.299
REFUGE+FOREST+AREA	5	883.2	895.2	5.0	0.026	0.298
REFUGE+OPENH2O+AREA	5	883.2	895.2	5.0	0.026	0.297
REFUGE+FOREST+SCSH+AREA	6	881.2	896.1	5.9	0.017	0.334
REFUGE+NPE+AB+FLOAT+AREA	7	879.1	897.1	6.9	0.010	0.373
REFUGE+AB+FLOAT+AREA	6	882.3	897.2	7.0	0.010	0.315

Figure 1. From top to bottom: 1) Photograph of Crane Lake from October 1950, showing expansive beds of submersed and floating-leaved vegetation; 2) GIS map of wetland vegetation at Crane Lake during 1955 showing aquatic bed (yellow) and floating-leaved (hatched blue) vegetation, and; 3) photograph of Crane Lake taken in September 2003 showing sparse vegetation (white spots are pelicans).

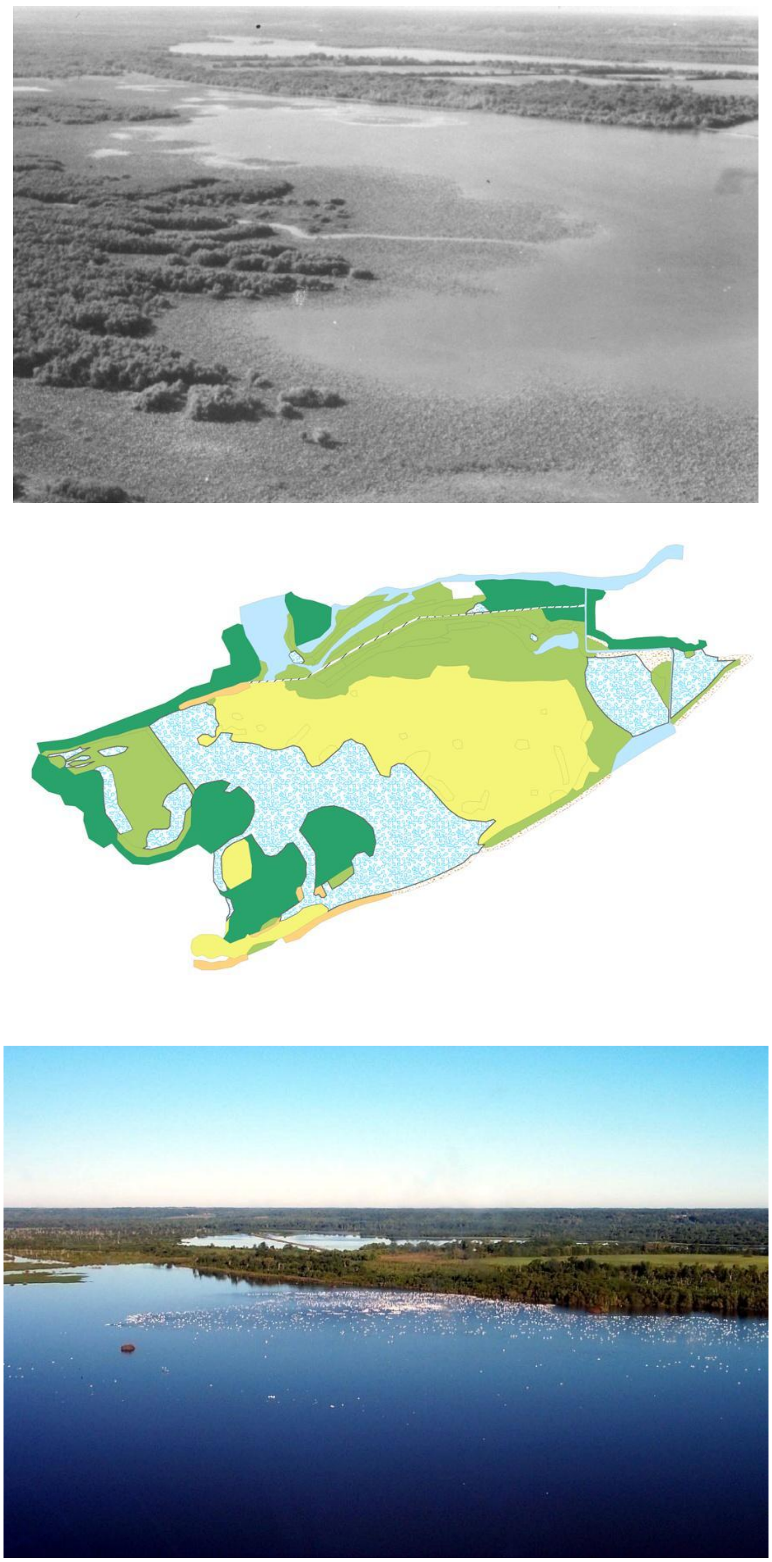
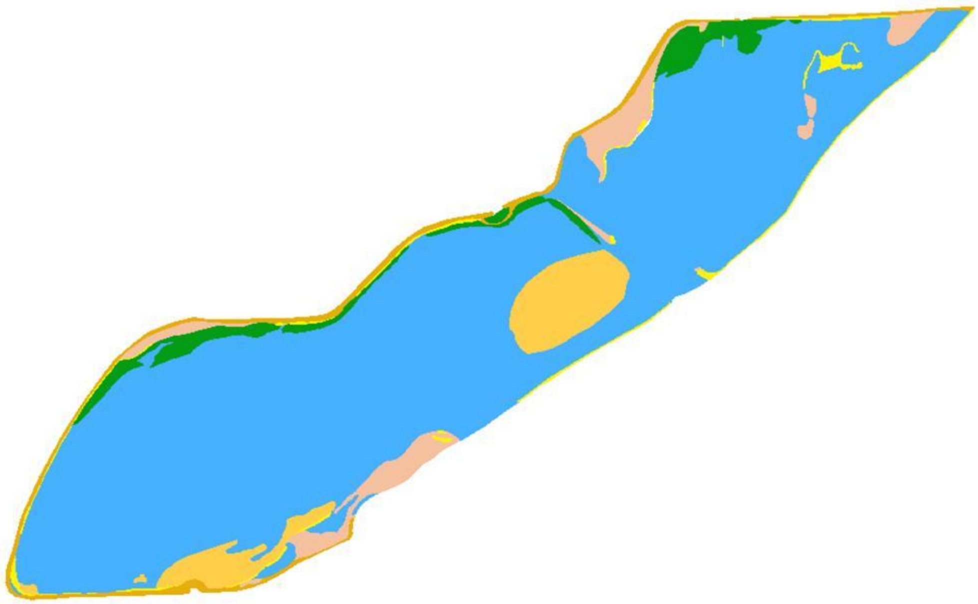
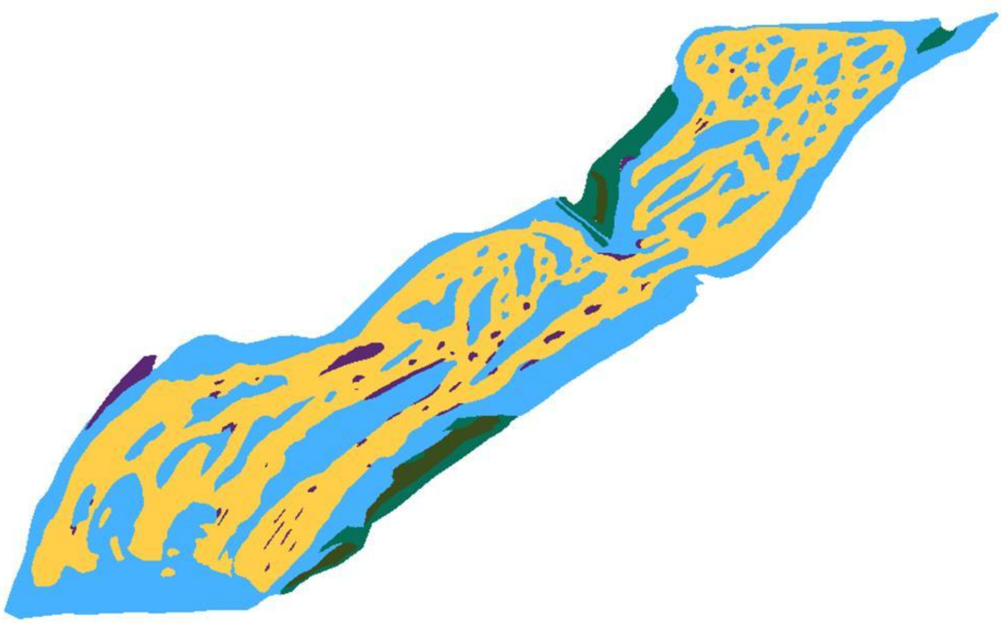


Figure 2. Maps of Chautauqua National Wildlife Refuge depicting different values of the interspersion and juxtaposition index (IJI). The IJI was least in 1955, when most vegetation was contained in the wetland periphery, and greatest in 1959 when submersed aquatic vegetation (yellow) was spread throughout the wetland. Maps were produced from ArcGIS shapefiles that were converted to grids (10 m pixels).



1955 (IJI = 45.7)



1959 (IJI = 85.2)

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